

Heteroclinic Chaos, Chaotic Itinerancy and Neutral Attractors in Symmetrical Replicator Equations with Mutations

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A replicator equation with mutation processes is numerically studied. Without any mutations, two characteristics of the replicator dynamics are known: an exponential divergence of the dominance period, and hierarchical orderings of the attractors. A mutation introduces some new aspects: the emergence of structurally stable attractors, and chaotic itinerant behavior. In addition, it is reported that a neutral attractor can exist in the $\mu \rightarrow +0$ region.

KEYWORDS: chaotic itinerancy, replicator dynamics, Lotka-Volterra equation, heteroclinic cycle, mutation

The replicator equation was initially proposed by Maynard Smith,¹⁾ and was developed thereafter to describe evolutionary dynamics (see e.g. Hofbauer²⁾). It is equivalent to the Lotka-Volterra equation,³⁾ and is now widely accepted as a basic model equation with applications ranging from ecosystems to other hierarchical network systems.

Recently, unexpected rich behaviors have been found in the equations.^{4,5)} Of these, the emergence of an exponential time scale and of a complex attractor hierarchy are worth noting. The phenomenon of long-time dominance by a unique variable (species) and a chaotic transition from one dominant species to another are generic features of the equation. The lifetime of the dominant species is found to diverge exponentially. This specific behavior is due to the heteroclinic cycles embedded in the replicator equation. Depending on one parameter, heteroclinic cycles can be hierarchically organized.

On the other hand, the heteroclinic cycle has been considered to be unrealistic in the light of biological systems. For example, a population size that decreases to the order of $O(e^{-100})$ is considered to be unnatural in a real ecosystem. One remedy for this is to set a lower bound to the population size, as in the work of Tokita and Yasutomi.⁶⁾ That is, a species whose population drops below the given threshold must be removed from the system. As a result, the system in the end attains a stable distribution of species. However, as a consequence, the system loses its rich temporal behavior and many degrees of freedom.

In the present letter, we propose another remedy: namely, to recover structural stability by introducing diffusion terms (see also^{7,8)}). The diffusion terms can be identified as immigrations and mutations in an ecological system. We report on the emergence of heteroclinic chaos, chaotic itinerant phenomena, and neutral attractors in the replicator equation with mutation.

Most studies on relatively large replicator equations deal with a random interaction matrix.^{4,5,6,7,8)} This often makes it difficult to analyze the mechanism controlling the generic dynamical behavior. Here we introduce a symmetrical interaction matrix, and use a Lotka-Volterra-type equation. These two types of equations are mutually transformable. We use a Lotka-Volterra-type equation with seven degrees of freedom as the simplest model having more than one heteroclinic cycle.

$$\begin{aligned} \dot{x}_i = x_i [1 - x_i - a(x_{i+1} + x_{i+2} + x_{i+4}) \\ - b(x_{i-1} + x_{i-2} + x_{i-4})] \end{aligned} \quad (1)$$

where $x_i \geq 0 (i = 0, 1, \dots, 6)$. There are two characteristic parameters a and b , which satisfy the inequalities:

$$a > 1 > b, \quad a - 1 > 1 - b \quad (2)$$

This equation is a natural extension of May's system.⁹⁾ We will discuss a family of replicator-type equations which have several properties in common: 1) The $\mathbf{R}_+^7 (= \{\mathbf{x}|x_i > 0 (i = 0, \dots, 6)\})$ plane is kept invariant. 2) There are saddle-type fixed points ($\mathbf{e}_i = (0, 0, \dots, 1_i, \dots, 0)$) at the boundaries and one interior repeller-type fixed point, which is given by $\mathbf{q} (= \frac{1}{1+3a+3b}(1, 1, \dots, 1))$. 3) A null point gives a trivial fixed point ($\mathbf{o} = (0, 0, \dots, 0)$).

This equation has a symmetrical property in the sense that every saddle point \mathbf{e}_i has an equal number of incoming and outgoing directions of dimensionality one. For any i -th point, there are heteroclinic orbits from \mathbf{e}_i to $\mathbf{e}_{i+j} (j = 1, 2, 4)$.

As a result, there are seven saddle points and 21 heteroclinic orbits in this system. Each incoming direction is correlated to one of the outgoing directions of the other saddle point (see Fig.1). All the initial points, except $x_0 = \dots x_6$, will asymptotically converge to a network composed of the 21 heteroclinic orbits.

As was first explicitly pointed out by Chawanya,⁴⁾ we also numerically find exponential divergence of the dominance period in the neighborhood of saddle points \mathbf{e}_i

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Fig. 1. A diagram of all possible heteroclinic orbits with seven saddle points symbolized as $e_k(k = 0, 1, \dots, 6)$. Every saddle point has three incoming and three outgoing connections to/from other saddle points. For example, a saddle point e_1 has three outgoing connections to e_2, e_3 and e_5 and three incoming connections from e_0, e_4 and e_6 . It is worth noting that e_2, e_3 and e_5 compose another heteroclinic cycle of period 3, in addition to e_0, e_4 and e_6 . Because of this symmetry, each saddle point is taken to be equivalent. Thus, there exist three heteroclinic cycles which itinerate all the saddle points, but in a different order. They are drawn in different line styles.

even with this symmetric equation (see Fig.2,4). Two different kinds of transition order from e_i to e_j are obtained. The transition order from e_i to e_j becomes either chaotic (a), or periodic (b) with respect to initial state. Almost every case belongs to the chaotic case (a). In the following, we introduce a diffusion term into the equation. By doing this, any heteroclinic cycle is removed from the system. Instead, we have the ruins of such cycles and the hoping dynamics among them.

Fig. 2. Time vs. $\log x_i$, simulated with $a = 1.2$ and $b = 0.9$. The dominance periods in the neighborhood of each e_i are gradually extended. When x_i is sufficiently close to the maximum value (i.e. unity), the growth dynamics of neighboring species are well approximated by the linear curves. That is, they are expressed by $1 - b$ and $1 - a$ for $\frac{d}{dt} \log x_{i+j}$ ($j = 1, 2, 4$) and $\frac{d}{dt} \log x_{i-j}$ ($j = 1, 2, 4$), respectively.

Fig. 3. $t - \log x_i$: simulation run with the parameters $a = 1.2, b = 0.9, \mu = 10^{-6}$. It can be clearly observed that a lower bound exists to each population size, which is given approximately by $\frac{\mu}{a-1} \simeq e^{-12.2}$.

A possible diffusion process for mutation is introduced in the original replicator model as follows:

$$\begin{aligned} \dot{x}_i &= x_i [1 - x_i - a(x_{i+1} + x_{i+2} + x_{i+4}) \\ &\quad - b(x_{i-1} + x_{i-2} + x_{i-4})] - 6\mu x_i + \mu \sum_{j \neq i} x_j. \end{aligned} \quad (3)$$

Here we assume that there exists mutation from x_i to x_j in the ratio μ for all i and j . We call the diffusion

Fig. 4. The n -th recurrence time for visiting a saddle point e_i with parameters $a = 1.2$ and $b = 0.9$.

process as mutation since it describes the flow from one population to the others, if we assume that the variable x_i as the population size of the species i and all species has the mutually transitional genotypes.

The mutation process naturally gives a lower bound $L_\mu (\simeq \frac{\mu}{a-1})$ to each population size (Fig.3). Therefore, every equilibrium point (e_i) on the peripherals vanishes simultaneously. Consequently, heteroclinic cycles no longer exist. The exponential divergence of the dominance period is also suppressed.

It is also worth noting that introducing mutation rates makes the system structurally stable. Therefore, the numerical results are rather insensitive to the numerical method we used. At the same time, it is more reasonable to use a structurally stable model to describe natural phenomena. Those two issues are great advantage to study the replicator equation with diffusion over other models.

The equation is simulated numerically with the 4th order Runge-kutta method. Even the system is made structurally stable, we solve an equation of a logarithm of each variable x_j . Doing this, we can study the very lower mutation rate regions.

When the mutation rate μ is higher than $\frac{a+b-2}{14(1+3a+3b)}$, the internal equilibrium point q becomes stable, which gives a unique fixed point in this system. Below the critical value, the q is destabilized and three limit cycles appear. Dominant species appear cyclically in each limit cycle with a fixed but different order (+1, +2 and +4). Each limit cycle is inversely characterized by this order. All the initial states in the phase space (\mathbf{R}_+^7) will be attracted to one of these limit cycles in this parameter region.

By further decreasing the mutation rate, we see sequential period bifurcation of each limit cycle, each having three quasi-periodic attractors (T^2) at some point. Each attractor holds the “dominant species recurrence order” which characterizes the original limit cycles found in the higher mutation-rate regime. It is difficult to observe the higher order tori (T^n), and we instead observe the breakup of three T^2 , and the emergence of a strange attractor. The Lyapunov exponents are computed as a function of the mutation rate in order to quantify the observed route to chaos in Fig.5.

It is worth noting from Fig.5 that there are two qualitatively different chaotic attractors in the higher and lower mutation regimes: one with two positive Lyapunov



Fig. 5. $\log \mu - \lambda_i$: Lyapunov exponents computed for the parameters $a = 1.2$ and $b = 0.9$ by varying the mutation rates.

exponents, and one with a single positive exponent.

We can interpret both structures of chaotic attractors as a combination of three local attractors connected by chaotic dynamics. These local attractors correspond to the heteroclinic cycles embedded in the original replicator system without mutations.

The term *chaotic itinerancy* is used to describe a situation where there is a natural separation of local attractors and chaotic dynamics which connects those attractors via a higher dimension subspace.¹⁰⁾ That is, a state itinerates chaotically among local attractors.

If the local attractor itself is chaotic, it is difficult to distinguish whether the state is in or out of local attractors. This case is typified by a chaotic attractor with two positive exponents. On the other hand, if the local attractor is not chaotic, it is possible to specify the state simply from the time-evolution of the size of the population. When a state is outside the local attractors, the population size changes rather chaotically. Indeed, we observe that the three local strange-attractors degenerate to quasi-periodic states in the lower mutation regime, where the dynamics connecting the local attractors remains strange. Therefore, chaotic behavior and quasi-periodic behavior appear alternatively.

This picture is well demonstrated by computing the local Lyapunov exponents. While the system stays in the local quasi-periodic state, the three largest exponents are computed as $(0, 0, -)$. While in the transition states, the exponents are computed as $(+, 0, -)$. Further, we estimate the local Kolmogorov-Sinai(KS) entropy¹¹⁾ to quantify the effective degrees of freedom at each moment. The local KS entropy is estimated by the sum of the local Lyapunov exponents with positive values. The local Lyapunov exponents are computed from the local Jacobian of the dynamics.

$$(local)KSE = \sum_{n=1}^q \lambda_n \quad (\lambda_q > 0, \lambda_{q+1} \leq 0) \quad (4)$$

The time series of the local KS entropy is plotted in Fig.6, where intermittent bursts of the KS entropy are clearly observed. It is seen from this figure that the switching between local attractors is associated with a burst of the local KS entropy. Since the behavior of the local KS entropy is almost the same as that of the number of the positive local exponents, we argue that this

switching behavior is followed by an increment in the number of effective degrees of freedom. From this characterization, we insist that the switching behavior found in this system should be named *chaotic itinerancy*.

Fig. 6. t - *localKSE*: Local KS entropy is computed under the condition $a = 1.2, b = 0.9$ and $\mu = 10^{-6}$. Where the local KS entropy is near zero, the orbit is in the neighborhood of one of the three local attractors. On the other hand, where the local KS entropy is large and positive, the orbit is in a transition state between local attractors.

In the limit of $\mu \rightarrow +0$, the original heteroclinic behavior is restored. Without any mutation terms, the system can show exponential growth of a single-species dominance period at $\mu = 0$. On the other hand, we know that even a small mutation rate can remove the heteroclinic cycles (i.e. there emerges a lower boundary to a population size denoted by L_μ). Therefore, we expect that $\mu = 0$ is a singular point. When we approach the point from the above (i.e. $\mu \rightarrow +0$), the largest exponent will approach zero. This implies that the expected dynamics becomes no more chaotic at this limit. Indeed, we see three different periodic behaviors which correspond to three heteroclinic cycles of the original replicator equation. Those periodic behaviors are thus indexed by a recurrent order of the dominant species(i.e. +1, +2 and +4). It is worth noting that the motions with the same recurrence order densely construct a partially disconnected torus. That is, the limiting behavior is constrained on the torus. In the following we analyze the situation.

Assuming that the mutation rate is infinitesimally small, we can approximate the dynamics by some linearized equations. The limiting behavior means that the orbit is well characterized by the transition between saddle points, and the approximation holds good enough around saddle points. There, the growth term $\frac{d}{dt} \log x_i$ is well approximated by $1-a, 1-b$ and 0 for the incoming, outgoing, and the dominant species, respectively. It is numerically found that each species becomes dominant twice, and diminishes (to the lowest order) four times during one period of time (see Fig.7). This is a necessary feature in order to keep the periodicity of this linearized equation. It can be rewritten more formally in terms of successive dominance periods of given species, which are denoted by t_1 and t_2 (see Fig.7 for the meaning).

$$(1-b)t_2 + (1-a)t_1 \leq 0, \quad (5)$$

$$(1-b)t_1 + (1-a)t_2 \leq 0, \quad (6)$$

$$t_1 + t_2 = -\frac{\log L_\mu}{(1-b)}. \quad (7)$$

Fig. 7. With sufficiently small μ , the growth factor $\frac{d}{dt} \log x_i$ is approximated by $1-a$, $1-b$ and 0 for the incoming, outgoing, and the dominant species, respectively.

The first and second inequality is derived by the fact that each species has to be at the lower boundary before it starts to dominate the population again. The third term is derived in order to hold the periodicity. That is, the sum of t_1 and t_2 should be conserved by the dynamics, but its ratio $\frac{t_2}{t_1}$ can be redundant under the following condition:

$$1 \leq \frac{t_2}{t_1} \leq \frac{a-1}{1-b} \quad (t_1 \leq t_2). \quad (8)$$

Within this range, absolute values of t_1 and t_2 can be freely determined. This degree of freedom gives a neutral direction of the periodic state. That is, the periodic state can exist infinitely many.

The above inequalities further set limits on where those periodic states can be found. We already know that there are three kinds of periodic cycle with respect to the recurrence order of the dominant species (+1, +2 and +4). Each of those three cycles can exist infinitely and being found on the unique torus. However, they have to coexist on the torus and the boundaries between different cycles are given by the inequalities. Namely, $(a-1)/(1-b)$ gives the maximal axial length of the partial torus size, where each cycle can occupy. Therefore, the torus is fragmented into three parts, each corresponds to different cycle state (in Fig.8(a)).

Even with a small mutation rate, we see that the dynamics takes off from the torus. The neutral directions discussed above does not exist anymore. The dynamics with the finite mutation rate is illuastrated in Fig.8(b). The periodic orbit gradually shifts to the edges of the regions, and finally switches off to other regions via chaotic motions. The original periodic behaviors now become quasi-periodic.

In this letter, we have shown how mutation dynamics changes the behavior of the original replicator system. In particular, a chaotic itinerancy is noted. We understand phenomenologically that the dynamic behavior of this system is well described by the composition of local attractors, and hoping between them, where the local attractors are ruins of heteroclinic cycles.

This system is made symmetric so that each saddle

(a) (b)

Fig. 8. A schematic drawing of the dynamics at $\mu \rightarrow +0$ (a) and at $\mu = +\epsilon$ (b). An orbit asymptotically converges to a cycle on a transverse direction of this torus at $\mu \rightarrow +0$. But with a small mutation rate, the orbit will no longer stay in one portion of the torus, but switches from one to the other. The switching behavior appears to be chaotic.

point has an equal number of incoming and outgoing connections to other saddle points. Understanding a bifurcation diagram and the limiting behavior was possible due to the symmetry of the system.

What we have observed in this system is not restricted to the present symmetrical cases. Replicator systems with partially disordered bimatrix have been studied, and the corresponding behavior has been reported (8)). A direct extension from this system is to study a series of symmetric equations with more than three local attractors. We would then expect that the chaotic itinerant dynamics could be in two ways: chaotic transition dynamics in time and in space. Not only the duration under the influence of one local attractor becomes chaotic, but so does the selection of the next-switching attractor. A detailed description of these systems including more than three local attractors will be reported elsewhere.

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